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Running header: Spatio-temporal configuration of roaring

Spatio-temporal variation in African lion roaring in relation to a dominance shift

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18 Roaring is an integral component of African lion (*Panthera leo*) ecology as it facilitates social
19 cohesion and territorial defense. Despite the importance of roaring, there is a limited
20 understanding of the configuration of this behavior in spatio-temporal dimensions. Here, we
21 mapped the configuration of lion roaring at the home range scale and quantified temporal
22 signatures in roaring frequency. We tested whether spatio-temporal patterns of roaring vary with
23 position within a lion dominance hierarchy using a dominance shift that occurred in a
24 reintroduced group of lions. We collected spatially-explicit roaring data from continuous follows
25 of 6 telemetered lions in Addo Elephant National Park, South Africa, for a 24-month period after
26 release. We assessed the frequency and location of roaring before and after a dominance shift.
27 We developed utilization distributions to describe space use at the coalition level for males and
28 individually for females. We plotted the frequency of roaring for these coalitions and females as
29 a group in each period. The spatio-temporal patterns in roaring were closely tied to social
30 dynamics and the eminent dominance shift experienced in this population. These patterns
31 highlighted a distinct shift in roaring strategy, especially in the newly subordinate male coalition,
32 which substantially reduced their roaring from 10 to ~ 3 roars per follow, altered their space-use,
33 and altered the spatial configuration of their roaring behavior from the periphery of their home
34 range when they were dominant to nearer to the core (averaging $\leq 31^{\text{st}}$ percentile) of their home
35 range when they became subordinate. While our findings were based on a limited sample, our
36 study suggests that the spatial strategy and frequency of roaring varies in relation to social rank
37 and patterns in space use of rival coalitions.

Key words: behavior, dominance, home range, lion, *Panthera leo*, roaring, South Africa, utilization distribution

Vocal communication is a fundamentally important suite of behaviors for numerous taxa around the globe. Auditory calls serve a variety of purposes and can communicate an individual's condition, fitness, and information on intra- and inter-group dynamics (Davies and Halliday 1978; Clutton-Brock and Albon 1979; Kitchen et al. 2003; Reby & McComb 2003; Fischer et al. 2004; Déaux et al. 2016). In lions (*Panthera leo*), communication is exceedingly important given the social and behavioral complexity of this species. Lions are the only group-living species in the family Felidae and exhibit a high degree of sociality, which has likely evolved because of the advantages garnered from collaboratively defending, expanding, and inheriting territories (Mosser et al. 2015). As both a social and territorial species, communication is essential to lion ecology and roaring is perhaps the most important vocal cue (Schaller 1972; McComb et al. 1994; Grinnell and McComb 1996; Frey and Gebler 2010). Roaring is integral to maintaining social cohesion, defending territory, and gathering information about the relative state of conspecifics (McComb et al. 1993, 1994; Grinnell and McComb 1996). Lions can also discriminate between resident and non-resident lions (McComb et al. 1993), determine the relative risk of encountering unfamiliar lions, and detect the ratio of residents to intruders from roaring choruses (Grinnell and McComb 1996). Thus, for male lions, roaring is a means to deter rivals, defend pride resources, and increase the opportunity of siring cubs in neighboring prides (Funston et al. 1998). However, the relative importance of roaring behavior has primarily been assessed via playback experiments (see McComb et al. 1993; Grinnell et al. 1995; Grinnell and McComb 1996, 2001; Spong and Creel 2004). Outside of research using simulated playbacks,

61 comparatively little information is known of the spatio-temporal factors that affect where and
62 when lions roar.

63 The spatio-temporal dimensions of lion roaring are expected to matter a great deal to lion
64 ecology. For instance, roaring is not only energetically expensive but it can also be dangerous.
65 The auditory effect of roaring is limited by distance (Bertram 1973; Funston 1999) and can
66 reveal one's location at potentially risky times (Grinnell and McComb 2001). Male lions also
67 investigate unfamiliar roars (Grinnell et al. 1995), making roaring a fundamentally important
68 behavior in territorial disputes (Grinnell and McComb 2001; Spong and Creel 2004). Thereby,
69 male lions are expected to increase roaring frequency near territorial boundaries, specifically in
70 the buffer zone adjacent to neighboring prides (Lehmann et al. 2008). But dominance is also
71 expected to play a role in where and when lions roar. For instance, dominant (resident) males
72 regularly roar but will often remain silent when they roam into regions outside of their
73 established territories, whereas subordinate (nomadic) males rarely roar at all, regardless of
74 location (Grinnell and McComb 2001). Thus, aspects of the dominance hierarchy should affect
75 where and when lions elect to roar.

76 We tested whether the frequency and location of roaring changed in a population of lions
77 for 2 years following a reintroduction. Specifically, we tracked 6 lions (4 males, 2 females) in
78 Addo Elephant National Park, South Africa. We examined roaring behavior of these lions in
79 relation to a dominance shift, occurring mid-way through our study, to measure variation in
80 roaring frequency and spatio-temporal patterns in roaring behavior throughout this landscape. To
81 our knowledge, we are not aware of any studies that have assessed territorial behaviors relative
82 to changes in social hierarchy. We hypothesized that dominant lions will roar more frequently
83 and that subordinate lions will roar less and avoid roaring in close proximity to dominant males.

Here, we 1) quantified the configuration of roaring for each male and female group at the home range scale, 2) identified temporal trends in the frequency of roaring, and 3) assessed changes in the spatio-temporal configuration of roaring in relation to a dominance shift. We discuss the implications of this research for the behavior and sociality of lions.

Materials and Methods

Study area. — From 2003 to 2005, we studied the roaring behavior of lions in Addo Elephant National Park (Addo; 33°30'S, 25°45'E) located north of Port Elizabeth, Eastern Cape Province, South Africa. The Main Camp (132 km²) section of Addo is separately fenced with the dominant habitat type being thicket interspersed with grassland stemming from the agricultural history of this land (Tambling et al. 2012). In total, the Main Camp section of Addo features 6 vegetation classes: gully thicket, thicket, bushclumps, short grassland, long grassland, and zuurkop woodland. Addo is unique because it lacks distinct wet and dry seasons. Rainfall occurs throughout the year but is often variable, featuring heavy rains and extended dry periods (annual rainfall is ~400 mm; Smit et al. 2016). Elevation in Addo ranges from 60 to 350 m above sea level. Lions and spotted hyenas (*Crocuta crocuta*) are the main carnivores in the study area.

Mapping roaring behavior. — We fit all lions ($n = 6$) with VHF-GPS telemetry collars to track their movement and roaring behavior. Collars were programmed to record a GPS location once every 4 hours. Anesthesia and collar attachment were carried out by the conservation and veterinary staff of South African National Parks under methods that were approved by the SAN Parks research ethics committee (Project No. 2004-03-01GKER) and followed the guidelines proposed by the American Society of Mammalogists (Sikes et al. 2016). Via telemetry-tracking, we conducted 96-h continuous follows of each lion to identify the spatial location and frequency of roaring behavior approximately once every 6 weeks for 2 years post-release (2003-2005).

Timing and locations of roars were recorded for each individual when observed. Using established criteria, we defined a roar as a bout of 1 or more moans followed by full roars and ending in a series of grunts (Stander and Stander 1988). In addition to the roaring behavior collected during our continuous follows, we also considered roaring bouts that we acquired opportunistically. These additional data were recorded during our study of hunting behavior of these lions and comprised a small proportion of our overall data on roaring (see Hayward et al. 2009).

We temporally partitioned spatially-explicit roaring data into 4 periods each spanning 3 months (beginning in December 2003 and ending in May 2005). Thus, this temporal partitioning aligns with a previous study of ours in which we documented temporal changes in home range size of lions, where larger home ranges were observed in winter months compared to summer (Hayward et al. 2009). Partitioning was also strategic in that it delineated the temporal extent of our study into equal-sized periods before and after the dominance shift, allowing for a 6-month (June to November 2004) intermediate period when the northern and southern male coalitions were grappling for dominance. Since we were primarily interested in changes in spatio-temporal behavior of lions relative to social status, we excluded this intermediate period from consideration due to frequent bouts between coalitions and difficulty in determining a clear dominant and subordinate male coalition.

Reintroduction and establishing dominance — In 2003, 6 unrelated lions (4 males, 2 females) were reintroduced to the Main Camp section of Addo after an approximately 100-year absence of lions from this system (Hayward and Hayward 2006). Lions were obtained from the Kgalagadi Transfrontier Park and separated into 2 groups, each consisting of 2 adult males and 1 adult female, prior to release with the aim of establishing 2 prides (Hayward et al. 2007).

Initially, lions were kept in bomas in the northern (2 males [Kalahari and Tsama] and 1 female [Kamqua]) and southern (2 males [Bitterbal and Nossob] and 1 female [Aardlam]) portions of the park before being released in December 2003.

Immediately following release, all 4 male lions and the female from the northern boma coalesced into a single group. Although all males were in close proximity, high levels of association were still observed among lions that had shared a boma at the time of release. Thus, 2 male coalitions were clearly evident, which existed for the duration of our study. The northern coalition consisted of Kalahari and Tsama, while the southern coalition included Bitterbal and Nossob. The other female, Aardlam, remained primarily nomadic after reintroduction and rarely interacted with the other 5 lions throughout the study. Initially, the northern coalition of males appeared dominant as determined by numerous aggressive interactions with members of the southern coalition. However, after roughly 8 months, the overall group fractured when the 2 female lions came into estrus. There was increased aggression and a series of bouts among the northern and southern coalitions of males that culminated in a final challenge for dominance during the winter of 2004. The southern coalition eventually prevailed and retained dominance for the duration of our study.

We calculated the social rank of the male coalitions using David's index of social dominance (David 1987). This metric functions similarly to the Clutton-Brock Index (Clutton-Brock et al. 1979) but incorporates the outcome of aggressive interactions (i.e., number of wins and losses) and is considered to be an improved estimator of social hierarchy (Gammell et al. 2003). We defined an aggressive interaction as a direct fight between 2 or more individuals, or facial or vocal aggression (Estes 1999), whereby 1 individual submitted or moved away from the other. We calculated David's index before and after the dominance shift to observe changes in

social rank of the coalitions. We did not use aggressive interactions that occurred within the same coalition in calculating this metric. Given similarities in movement and notable levels of association among individuals of a coalition, we conducted analyses of lion roaring at the coalition level. We also grouped females for comparative purposes and since we expected them to exhibit similar roaring strategies.

Quantifying temporal signatures of roaring. — To assess temporal signatures in roaring, we calculated the frequency of roaring during each observational period. We standardized these frequencies by the amount of observational effort for each group based on the number of continuous follows during each respective time period. This metric was then related to the number of roars per period, which functioned as a roaring per observational effort metric (i.e., number of roars per period/number of follows per period). This approach allowed for an unbiased assessment of the frequency of roaring among groups during continuous follows. We also conducted a linear regression of the average number of roars per follow and calculated the standard error for each lion group over the entire study. The goal of this regression was to observe general trends in roaring frequency.

Quantifying the spatial configuration of roaring. — We developed utilization distributions (UDs) to quantify the space use of male lions in each temporal period at the coalition level so as to depict the spatial configuration of roaring at the home range scale. For females, we generated UD's individually due to infrequent associations and differences in space-use. We used locational data for each male coalition and individual female to generate UD's at a resolution of 30 m², via the “ks” package (Duong 2015) in program R (3.2.2; R Development Team 2015). We calculated UD's using a bivariate plug-in matrix with smoothing parameters that estimated bandwidth across rotated axes. Next, we converted these UD's to percent volume

rasters (Marzluff et al. 2004; Montgomery et al. 2012, 2013). Lower percentiles (i.e., near 1%) of the UD represented areas in the core of the home range whereas higher values (i.e., near 95%) corresponded to the perimeter.

We intersected the roaring locations with the respective UD raster to quantify the percentile associated with each roar. Next, we calculated the average UD percentile of these roars across each observational period. We conducted non-paired *t*-tests to assess potential differences in the roaring strategies exhibited by each lion group before and after the dominance shift. Percentiles of each roaring location in the first 2 periods and last 2 periods were combined to create groupings by “before” and “after” the dominance shift. Non-paired *t*-tests were then performed to compare differences in the location of roaring before and after the dominance shift for each group.

RESULTS

We radio-tracked and monitored the roaring behavior of lions for 24 months following their reintroduction to Addo. We observed a total of 35 aggressive interactions among lion coalitions. Between December 2003 and the winter of 2004, the northern coalition won a majority of the bouts (Table 1). Aggressive interactions occurred more frequently in the winter of 2004 leading up to the dominance shift, with the southern coalition prevailing in each. David's index indicated a transition in social dominance from the northern coalition prior to winter 2004 to the southern coalition after winter 2004 (Table 1).

We conducted 88 continuous follows of lions and observed a total of 438 roaring events (Table 2 – 3). On average, we conducted 8 continuous follows of the male coalitions and 6 for the females per observational period. The average number of roaring events was 36 (SE = 14.16; range 0 – 173) per group and period. Using the 4,561 spatial locations of lions returned from

radio-tracking (Table 3), we developed UD_s at the coalition level for males and individually for females across each of the 4 observational periods. The mean 95% home range size was 30 km² (SE = 5.96) for the southern coalition and 27 km² (SE = 3.40) for the northern coalition. Home range size was relatively larger for females, both averaging 38 km² (Aardlam SE = 9.69; Kamqua SE = 12.17). For both females, home ranges were largest immediately following the dominance shift, most notably for Kamqua. After the dominance shift, the northern coalition displayed the smallest home range (18 km²) for males observed in our study. During this same time period, the southern coalition had the largest home range that we observed among males (44 km²).

When assessing the number of roars per follow before and after the dominance shift, the frequency of roaring changed for each male coalition. Directly after reintroduction, roaring was comparatively low (0–1 per follow) for all lions. However, between 3–6 months after release, roaring became comparatively common (i.e., $\bar{x} = 8.49$ roars per follow for all lions; Fig. 1). However, we documented considerable variation in roaring. In period 3, after attaining dominance, the southern coalition roared more frequently whereas roaring in the northern coalition decreased and remained relatively low for the duration of the study (Fig. 1). This pattern was most noticeable in period 4 when the southern coalition averaged 19 roars per follow whereas the northern coalition averaged just 3 roars per follow (Fig. 1). The frequency of roaring by females also was low (≤ 6 roars per follow) and decreased slightly after the dominance shift (Fig. 1).

The spatial configuration of roaring at the home range scale varied by observational period and coalition. Throughout this study, the average UD percentile where roaring occurred was the 47th percentile. This measure was calculated across periods and lion groups. There were

changes in the location of roaring in all lion groups before and after the dominance shift indicating changes in the roaring strategy according to our non-paired *t*-tests. For example, roaring in the southern coalition occurred more often at higher percentiles, or nearer to the periphery of their home range. The location of roaring within the home range of this coalition differed before and after the dominance shift ($t_{254} = 5.34$, $P = <0.001$) with roaring being more concentrated near mid-level percentiles after achieving dominance (Fig. 2). The northern coalition experienced a distinct change in roaring strategy after the dominance shift, with increased roaring near the core of their home range ($t_{101} = 5.31$, $P = <0.001$; Fig. 2). Females displayed a relationship similar to that of the northern coalition, by roaring more near the core of their respective home ranges after the dominance shift ($t_{20} = 6.18$, $P = <0.001$; Fig. 2).

Evaluating the UD_s for each coalition revealed differences in the space use of lions, both temporally and by coalition. In observation period 1, space use was relatively comparable for each coalition, with minimal roaring occurring during this period and movement being concentrated in the northeastern portion of Addo (Fig. 3). In observation period 2, core-use areas of the northern and southern coalitions differed, with each group favoring the northern and eastern portions of the park, respectively. Differences in space use among male coalitions was most pronounced immediately following the dominance shift (observational period 3). During this time, the southern coalition favored the northern portion of the park whereas the northern coalition remained in close proximity to the southern fenceline. However, contrasting space-use patterns were less distinct during period 4, with all lions favoring the southeastern park boundary (Fig. 3). Throughout most of the study, movement patterns exhibited by the northern coalition more closely mirrored those of the females, with the lone exception occurring in observational period 4 (Fig. 3).

DISCUSSION

Among a reintroduced population of lions, we found that roaring by males changed in relation to an evident dominance shift. Specifically, the male coalition that became subordinate substantially reduced their roaring, altered their space-use, and displayed a tendency to roar near the core of their home range rather than near the periphery. Immediately post-reintroduction, we found that roaring by lions was relatively infrequent. This result likely reflects acclimation to Addo, where individuals attempted to find and establish a territory. Lions are often timid post-reintroduction, with animals remaining close to a release site (Hunter 1998) and slowly exploring the surrounding areas (Killian and Bothma 2003). These observations are consistent with non-reintroduced lions that will remain silent when outside of their established territories or in unfamiliar areas (Grinnell and McComb 2001). Similar levels of caution likely influenced the amount of roaring early in our study. Our results suggest that it takes ~3–6 months for lions to begin actively roaring in a reintroduced area. This behavior likely reflects individuals becoming acclimated to their surroundings and jockeying for territory amongst other lions in Addo. We believe the timing of this phenomena is directly related to the size of the area selected for reintroduction. Given that the Main Camp section of Addo is a small (132 km²), fenced reserve, this acclimation stage is likely quicker than what may be observed in other, larger areas. Despite calls for research on the behavior of reintroduced carnivores (Somers and Gusset 2009), much is yet to be learned on how behavior differs between reintroduced animals and their wild conspecifics. Additional research will help elucidate the behavioral strategies used by reintroduced carnivores and can aid in assessing population health in managed reserves.

We observed compelling temporal trends in the frequency of lion roaring that highlight changing strategies amid social strife. Prior to the dominance shift, roaring increased among all

groups of lions, with the southern coalition roaring at a slightly higher rate than the northern coalition. This difference potentially forecasted the upcoming challenge and eventual dominance take-over by the southern coalition. Other behavioral studies of lions also have observed higher frequencies of roaring prior to a challenge for dominance (Grinnell and McComb 2001). After the dominance shift, the southern coalition roared more frequently than the other groups in the study site. This result is consistent with research indicating that roaring is influenced by social rank, where nomadic males roared infrequently in comparison to established resident males (Funston 1999; Grinnell and McComb 2001). Other species also are known to alter behavior and lower the frequency of calls when running the risk of being heard or encountered by rival conspecifics (gray wolves, *Canis lupus*—Harrington and Mech 1979; chimpanzees, *Pan troglodytes*—Goodall 1986; coyotes, *Canis latrans*—Gese and Ruff 1998; Galápagos sea lions, *Zalophus wollebaeki*—Kunc and Wolf 2008). Additionally, movement of lions was limited by the fences in the Main Camp section of Addo, which reduced the ability of the northern coalition to disperse when they became subordinate. This limitation resulted in a potentially artificial increase in home range overlap with the dominant coalition and likely exacerbated the need for subordinate lions to roar infrequently. Overall, our results confirm similar findings that the rate of roaring in lions is contingent upon location and social rank.

We detected significant differences in the spatial roaring strategy of male lions before and after a dominance shift. It has been previously reported that lions will alter their roaring when near rival conspecifics, suggesting that this behavior is closely related to proximity and social hierarchy (Grinnell and McComb 2001), but this pattern had yet to be rigorously quantified. The spatial strategies we observed support this hypothesis. Space-use and roaring strategies were most similar among all lions immediately following reintroduction to Addo, with

all lions roaring near the periphery of their respective home ranges. This strategy was likely due to an uncertain social hierarchy that would inevitably be challenged as the lions became acclimated to Addo and established territories early in the study. This strategy also would lessen the likelihood of being heard and attracting the attention of dominant males, and aligns with findings from previous research. Grinnell and McComb (2001) observed similar low rates of roaring by nomadic male lions in comparison to resident males, especially when outside of their respective territory. Behaviorally this strategy seems intuitive, given that roaring in close proximity to resident males not only increases your likelihood of being heard and reveals your position, it also leads to conflicts among coalitions, which in some instances can result in death (Schaller 1972; Grinnell et al. 1995). Additionally, the southern coalition favored roaring in areas nearer to the periphery of their home range. Due to the amount of home range overlap between the southern and northern coalitions, this strategy likely reflects a preference for territorial advertisement in areas that are shared between the 2 coalitions. This result would align with findings by Lehmann et al. (2008) that indicated a similar pattern of roaring in shared buffer zones between neighboring coalitions. It also would indicate that movement and roaring behavior is likely influenced by pre-existing social hierarchies as suggested by Benhamou et al. (2014).

This study provides one of the first attempts to assess the spatio-temporal configuration of roaring in lions. We also had the unique opportunity to observe behavioral changes in relation to a dominance shift. We quantitatively supported findings on the behavioral ecology of lions that have been primarily anecdotal to this point. Although our analysis reveals interesting trends, our findings are based on a limited sample and we encourage additional investigation on this topic to strengthen conclusions. In this study, we specifically analyzed roaring; exploration into

other territorial behaviors (i.e., marking) in this species could provide additional interesting results. Spatio-temporal analyses of behavior have rarely been applied to mammals but could offer valuable explanations about why behaviors occur and inform ecological theory in other species. Such studies could be useful for species whose life history relies heavily on a particular behavior, or a behavior that is essential to social dynamics. Our study was conducted on a population of reintroduced lions, which may have influenced some of the patterns that we observed. However, prior studies of the reintroduced lions of Addo have been yielded results similar to studies of other wild populations in terms of home range size and prey selection (Hayward et al. 2009). Furthermore, small and intensively managed reserves, specifically in southern Africa, are one of the few areas where lion populations are stable (Bauer et al. 2015). Given the substantial decline in the lion populations of East, West, and Central Africa, increased research effort on reintroduced lions in successfully managed reserves may be essential for the persistence of this species. Our results provide information on how lions move, behave, and compete in a small wildlife reserve and can help to inform the management of this species in similar environments.

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Table 1. David's index (David 1987) of social dominance for male coalitions of African lions (*Panthera leo*) before and after a dominance shift in the winter of 2004 in Addo Elephant National Park, South Africa, 2003-2005. w = sum of proportion of wins, $w^{(2)}$ = sum of weighted proportion of wins of the coalition that was defeated, l = sum of proportion of losses, $l^{(2)}$ = sum of weighted proportion of losses of the coalition that was victorious.

Observation period	ID	Aggressive interactions ^a	w	$w^{(2)}$	l	$l^{(2)}$	David's index ^b
Dec. 2003–May 2004	Southern coalition	20	0.611	0.323	0.695	0.851	-0.612
	Northern coalition	21	0.528	0.682	0.472	0.646	0.092
Dec. 2004–May 2005	Southern coalition	12	0.625	0.188	0.750	0.188	-0.125
	Northern coalition	8	0.000	0.000	1.000	0.750	-1.750

^a Aggressive interactions include bouts between male coalitions and the female group

^b David's index serves as a relative ranking where higher values correspond to dominant individuals within the hierarchy

Table 2. Number of follows during each observation period per group of lions (*Panthera leo*) in Addo Elephant National Park, South Africa, from 2003-2005. Mean = average number of follows during entire study, SE = standard error of follows, n = number of lions per group.

Observation period	Southern coalition (n = 2)	Northern coalition (n = 2)	Female group ($n = 2$)
Dec–Feb 2004	8	6	12
Mar–May 2004	16	6	2
Dec–Feb 2005	5	10	2
Mar–May 2005	4	10	7
Mean	8.25	8	5.75
SE	2.72	1.15	2.39

Table 3. Summary of the social rank, number of roars, and GPS locations per observation period for each group of lions (*Panthera leo*) in Addo Elephant National Park, South Africa, from 2003-2005.

ID	Rank	Observation period	Number of roars (<i>n</i>)	Number of locations (<i>n</i>)
Southern coalition	Subordinate	1	3	252
		2	173	997
	Dominant	3	32	367
		4	77	388
Northern coalition	Dominant	1	0	256
		2	55	625
	Subordinate	3	35	344
		4	31	427
Female group		1	0	141
		2	11	278
		3	8	305
		4	13	181

- Figure 1. Frequency of roaring per follow for each group of lions (*Panthera leo*) in Addo Elephant National Park, South Africa, from 2003-2005. The vertical dashed line represents the relative timing of the dominance shift. Corresponding linear regression lines (dashed) and standard errors (shaded area) are provided in matching colors for each lion group.
- Figure 2. Distribution of roaring behavior within home ranges of lion (*Panthera leo*) coalitions in Addo Elephant National Park, South Africa, from 2003-2005. Height of bars indicates the average UD percentile where roaring occurred within a given observational period: lower values represent the core and higher values represent the periphery of the home range.
- Figure 3. Distribution of roaring locations within utilization distributions for each group of lions (*Panthera leo*) and observation period in Addo Elephant National Park, South Africa, from 2003-2005. Isopleths depict 5, 10, 25, 50, and 95 percent utilization distributions within home ranges. Rows represent lion group and columns portray observational period.